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They arrived and don't stop coming: an update on the distribution of exotic ants (Hymenoptera, Formicidae) in continental Ecuador

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Abstract. We present an updated list of introduced ants to continental Ecuador, and compile records of occurrence, as well as map the distribution of 15 exotic species. We analyzed specimens in entomological collections and data from AntWeb, GBIF and iNaturalist. Among these, we add two new records for the country: *Cardiocondyla mauritanica* Forel, 1980 and *Pheidole megacephala* (Fabricius, 1793). The former is also the first record for South America, while the finding of the latter shows how little we know about introduced tramp ants. In addition, we add site records for nine species: *Cardiocondyla emeryi* Forel, 1881, *Cardiocondyla minutior* Forel, 1899, *Cardiocondyla wroughtonii* (Forel, 1890), *Linepithema humile* (Mayr, 1868), *Monomorium floricola* (Jerdon, 1851), *Monomorium pharaonis* (Linnaeus, 1758), *Paratrechina longicornis* (Latreille, 1802), *Tapinoma melanocephalum* (Fabricius, 1793), and *Tetramorium bicarinatum* (Nylander, 1846). Based on our previous fieldwork observations, it appears that our understanding of exotic species richness is still in its early stages.

Keywords. Adaptation, biological invasions, citizen science, human disturbance, invasive species, tramp ants

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Introduction

Invasive species are those that can establish self-reproducing populations outside their native range and are agents of change in the ecosystems they inhabit (Dekoninck et al. 2019; IUCN 2020). Invasive species can also threaten native biodiversity by, for example, reducing populations of critically endangered taxa (Dueñas et al. 2021; Gentili et al. 2021; Fortuna et al. 2022), undermining recovery of species diversity (Matos et al. 2022), or acquiring and damaging new plant hosts (Sequeira et al. 2017). Over the last two centuries, the dispersal of invasive species to new sites has accelerated due to human activities such as the homogenization of habitats (Groffman et al. 2014) and the rapid connectivity of different landscapes. For example, fluvial and terrestrial transportation facilitates access to tourists and trade of products in Amazon human communities. Also, demographic growth and change of land use may facilitate new access routes for the introduction of alien species (Hulme 2009).

Social insects are amongst the worst invaders worldwide, and within this group ants contribute to a big portion (Bertelsmeier 2021). More than 200 species

have successfully established themselves outside of their native range, 19 are classified as highly problematic, and five are on the list of the top 100 worst invasive species (*Linepithema humile* Mayr, 1868, *Paratrechina longicornis* (Latreille, 1802), *Pheidole megacephala* (Fabricius, 1793), *Wasmannia auropunctata* (Roger, 1863), and *Solenopsis invicta* Buren, 1972) (Lowe et al. 2000; Suarez et al. 2010; Lach 2021).

Invasion by alien taxa is considered the second most common threat responsible for the extinction of species (Capdevila-Argüelles et al. 2013; Bellard et al. 2016). Invasiveness is facilitated by adaptations in morphophysiology, such as polygyny, intranidal mating, and little or no intraspecific competition because social-insect colonies may be separated although socially connected (Robinson 2014; Yang and Shoemaker 2021). These adaptations allow species to constantly reproduce, tolerate human disturbance, and grow massive colonies via continual colony founding (Holldobler and Wilson 1990; Holway et al. 2002), sometimes with a high capacity of unrestricted growth, like in the Argentine ant *Linepithema humile* (Moffett 2012).

The impacts of invasion by ants range from attacks to domestic animals (Aldana et al. 2013), displacement of native species (LeBurn et al. 2013), obstruction of human activities (Holway et al. 2002), and transport of certain pathogens (Lutinski et al. 2015). Invasive ants can induce declines in species richness, taxonomic homogenization, and phylogenetic clustering in native ant communities (Lessard et al. 2009).

While the environmental impacts of the top 100 invasive species has been widely documented, there is less knowledge about the economic impacts of many of these species. Consequently, quantification of the economic costs associated with biological invasions has lagged behind (Cuthbert et al. 2021). Furthermore, environmental impacts often lack a clear commercial dimension, making them difficult to accurately quantify (Hanley and Roberts 2019).

In InvaCost, the economic costs caused by 60 of the 100 worst invasive species were estimated at about $148.9 billion. Among these species, the ant *Solenopsis invicta* stands out as the most studied in this context, causing losses of around $16.7 million (Cuthbert et al. 2022).

In Ecuador, Von Aesch and Cherix (2005) were the first to monitor and study the behavior of invasive ants on Floreana in the Galápagos archipelago. They recognized 10 tramp species, but see also a revision by Causton et al. (2006). Donoso et al. (2014) published the first checklist of continental ants in Ecuador and included 10 invasive species in their list. Later, Pazmiño-Palomino et al. (2020) added *Nylanderia fulva* (Mayr, 1862) based on populations in sugarcane crops in Guayas province. Herrera et al. (2021) recorded nine alien species, both for continental Ecuador and the Galápagos. Finally, Padrón et al. (2022) provided an additional record of *Monomorium floricola* (Jerdon, 1851), which was collected in Ecuadorian southern Amazonia.

In addition to the lack of entomologists and biodiversity monitoring in tropical America, it also seems that there is little interest by researchers studying invasive species, despite the proven negative impacts of invasive species. From a worldwide view, most studies focus on invasive ant species in USA and Europe, while a handful of studies have been developed in Latin America, for example, in Colombia (Dekoninck et al. 2019).

To ameliorate this issue and increase our understanding of exotic ant species diversity in Ecuador, we have updated the list of introduced ants in continental Ecuador, compiling occurrence records of 15 previously recorded tramp species, and discuss their potential impacts on native biodiversity, as well as to humans.

Study Area

Ecuador is located in northwestern South America, bordering Colombia to the north, Peru to the south and east, and the Pacific Ocean to the west. It is the smallest of the Andean countries at 256,370 km^2, not including off-shore islands. It is crossed by the equatorial line, from which it gets its name, and extends between 01°30′N and 05°00′S and 075°20′W and 091°00′W (Neill 1999; Varela and Ron 2023). The Andes cross Ecuador from north to south and can be classified into two main mountain ranges, which reach altitudes of over 5000 m: the western cordillera and the eastern cordillera. They are linked by a series of transverse nodes that delimit inter-Andean valleys (Neill 1999). In the upper Amazon there are three branches of the Andes partially separated from the eastern cordillera: the Napo-Galeras, Kutukú, and Cóndor mountain ranges. The Amazon lowlands consist mainly of large valleys and lower elevation mountains (Varela and Ron 2023). As of 2013, the remaining native vegetation is 60,592 km^2 and the disturbed areas 46,055 km^2 (MAATE 2016).

Methods

The examined specimens are preserved in the following natural history collections: Colección de Entomología, Instituto Nacional de Biodiversidad, Quito, Ecuador (MECN); Colección de Invertebrados, Museo de Historia Natural "Gustavo Orcés V.", Escuela Politécnica Nacional, Quito, Ecuador (MEPN); and Entomology Collection, University of Texas at Austin, USA (UTIC).

To complement our species list we reviewed all online records of specimens collected in Ecuador from AntWeb (http://www.antweb.org), and we gathered Formicidae occurrence data from the Global Biodiversity Information Facility (https://www.gbif.org/) and iNaturalist (https://www.inaturalist.org). Up until March 2023, we examined all available image records and corroborated their identification to species by contrasting their morphological features with correspondent diagnostic characters whenever possible.

We transcribed to our working matrix the collection information associated to each specimen's label. In

addition, we used our own field notes, including information about behavior and biology of some species here treated. Geographic coordinates were verified using Google Maps (https://www.google.com/maps) and the World Coordinate Converter (https://ww.twcc.fr). We used QGIS v. 2.14 (QGIS Development Team 2016) for visualizing the distribution of species records, as well as for building the heatmap. Our point dataset is composed of all examined records per species. We used the raster layer "NE1_HR_LC_SR_W_DR" downloaded from Natural Earth (https://www.naturalearthdata.com/) for the base map. We downloaded the shapefiles (vector layers) of national and provincial borders from the Instituto Geográfico Militar (https://www.geoportaligm.gob.ec). We used a heatmap search radius (kernel bandwidth) of 2.7 million meters, with the Epanechnikov kernel shape for generating smooth hotspots. Map figures were saved as GeoTIFF, with final retouching using Adobe Illustrator v. 25.2.1 (Adobe Systems Inc.).

We used the following taxonomic treatments for species determination of most of the materials: *Pheidole* (Fischer and Fisher 2013; Sarnat et al. 2015; Salata and Fisher 2022), *Cardiocondyla* (Seifert 2003; Seifert et al. 2017; B. Seifert pers. com.), *Paratrechina* (LaPolla and Fisher 2013), *Monomorium* (Fernández 2007), *Tapinoma* (Guerrero unpub. data) and *Tetramorium* (García and Fisher 2011). Morphological terms follow Guerrero et al. (2019).

We took several differentially focussed images per specimen under a stereomicroscope Olympus SZ61R with attached digital camera (The Imaging Source DFK23UX236) using IC Measure v. 2.0.0.161 software. These images were then stacked in Helicon Focus v. 7.5.6 (Helicon Soft Ltd.). We used Adobe Photoshop CS6 for final retouching.

Morphometric body features cited in the text. CL = maximum cephalic length in median line. Taken from the posteriormost margin to the anterior clypeal margin, CW = maximum cephalic width, CS = cephalic size, FRS = distance of the frontal carinae immediately caudal of the posterior intersection points between frontal carinae and the lamellae dorsal of the torulus, PoOc = postocular distance, PpH = maximum postpetiole height, SL = scape length, SP = maximum length of propodeal spines (see Seifert 2022 for extended details).

Results

Cardiocondyla emeryi Forel, 1881

Figures 1, 10b

Materials examined. ECUADOR – **Pichincha** • Quito, Mitad del Mundo; −00.0021, −078.4563; 2425 m alt.; 07.XII.2003; A. Wild & J. Vieira leg.; active search; UTIC 00215111, UTIC 00215112 • Quito, Guayllabamba; −00.0700, −078.3573; 2162 m alt.; 09.VI.1984; A. Sancho leg.; active search; MECN-EN-HYM 3965 – **Loja** • Macará, Canguraca, Reserva Laipuna; −04.21056, −079.88682; 680 m alt.; 12.XII.2013; A. Castro leg.; active search; CISEC0005352; • Macará, Canguraca, Reserva Laipuna; −04.21056, −079.88682; 680 m alt.; 2.X.2014; M. Tuza, G. Vélez, G. Gómez, G. Piedra, J. Lattke leg.; active search; CISEC 0010124.

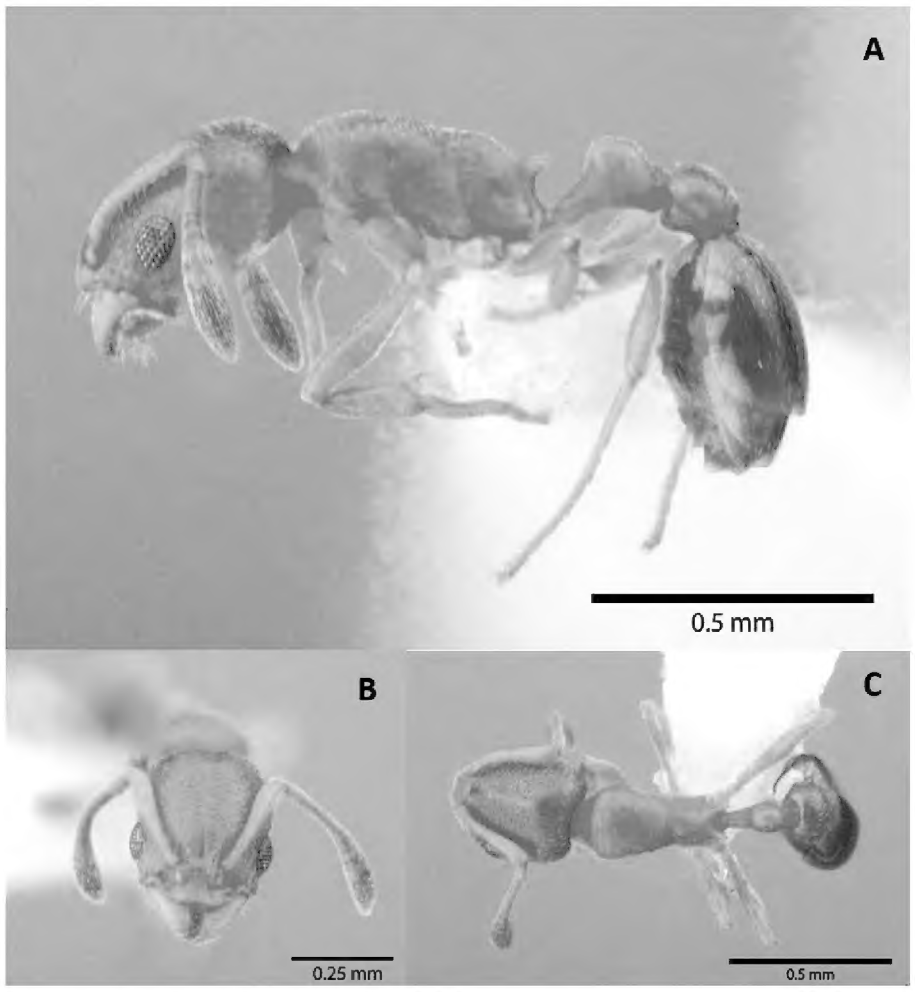

Figure 1. *Cardiocondyla emeryi* (UTIC215111). **A.** Lateral view **B.** Frontal view **C.** Dorsal view. Images by Alex Wild.

Identification. In dorsal view, head and mesosoma without longitudinal rugosity; median vertex with weak, interrupted longitudinal carinulae; surface of mesosoma with well-pronounced and dense microreticulum; in lateral view, promesonotum shallowly convex, not abruptly sloping into moderately deep metanotal groove; in dorsal view: petiolar node distinctly longer than wide, peduncle moderately long; postpetiole wider than long, with concave anterior margin and evenly convex lateral margin (Seifert 2003).

Common name. Emery's Sneaking Ant

Comments. Of the color variants, the most frequent variation has a yellowish body with blackish gaster, or sometimes the entire body is dark brown (Mackay 1995; Seifert 2003). Populations of this species can show polymorphism in microsculptures, which makes *C. emeryi* a species complex, in addition to the usual high intraspecific variability (Seifert 2003).

This species is native to the Afrotropics and occurs mainly in xerothermic habitats (Seifert 2003). We collected specimens in a garden around the Mitad del Mundo monument, an urban site within an Andean dry valley at 2600 m a.s.l.; this site is characterized by shrubby and thorny vegetation and is some 10 km north of Quito, the capital of Ecuador.

We found the oldest known record of this species from continental Ecuador in MECN, a specimen collected in 1984 in Guayllabamba. This town is also within an Andean dry valley, in habitat similar to that

at Mitad del Mundo. Lubin (1984) first reported *C. emeryi* in the Galapagos Islands, and later Von Aesch and Chreix (2005) confirmed its presence on Florena Island. Lattke et al. (2016) collected a few specimens in the province of Loja, southwestern Ecuador, at a xerothermic site at 680 m a.s.l.

***Cardiocondyla mauritanica* Forel, 1890**
Figures 2, 10c

Materials examined. ECUADOR – **Pichincha** • Quito, Mitad del Mundo; −00.0021, −078.4563; 2425 m alt.; 07.XII.2003; A. Wild & J. Vieira leg.; active search; UTIC00215113; UTIC00215114.

Identification. Head elongated, with small eyes; foveolae on vertex not separated by interspaces, deeply impressed; clypeus with few longitudinal rugae; mesosoma with well-developed microreticulum; first gastral segment completely glabrous; propodeal spines short and blunt; petiolar node slightly longer than wide in dorsal view; postpetiolar node somewhat hexagonal in dorsal view; sternite almost completely lacking (Seifert et al. 2017).

Common name. Moorish Sneaking Ant

Comments. This species prefers nesting in dry, open environments and, in some cases, in wet, sandy soils with decomposing organic matter (Sharaf et al. 2017). According to Seifert et al. (2017), the native range of *C. mauritanica* possibly extends from India, Pakistan, west to the Middle East, North Africa, and the Mediterranean. Worldwide, *C. mauritanica* is the most broadly distributed species in its genus (Seifert 2003); the populations from the Canaries, the Nearctic region, and Indonesia were probably introduced through international trade (Wetterer 2012a; Seifert et al. 2017). Here, we report the first records from continental South America; the specimens were collected in an urban garden at Mitad del Mundo.

This species shows strictly intranidal mating with polygynous colonies; as in *C. emeryi*, ergatoid males are common in *C. mauritanica* (Seifert et al. 2017).

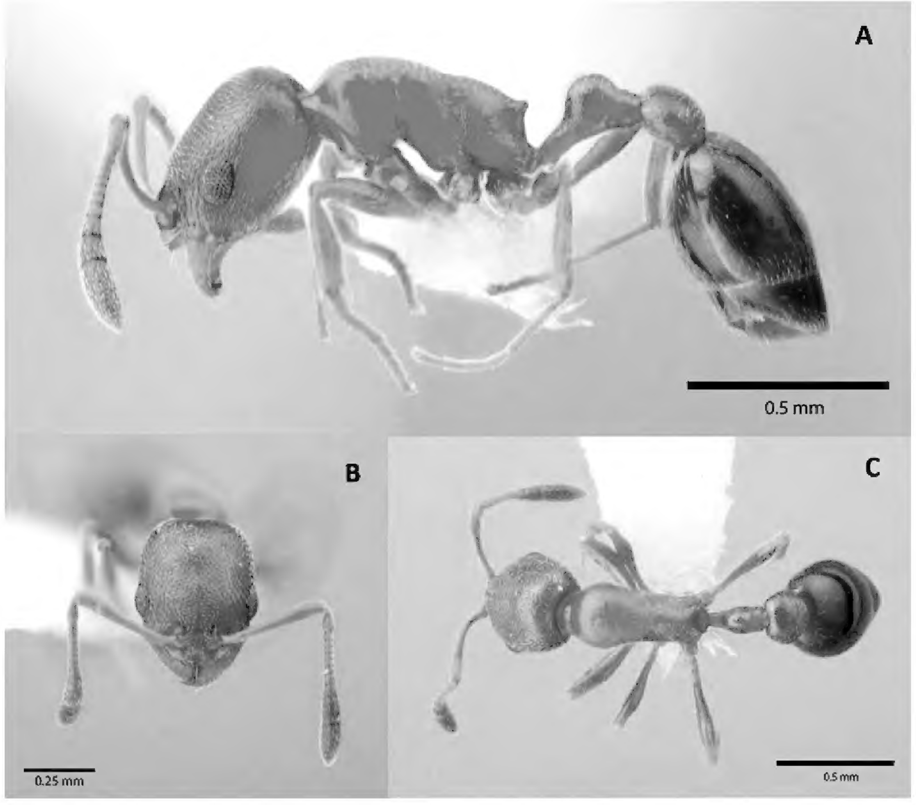

Figure 2. *Cardiocondyla mauritanica* (UTIC215114). **A.** Lateral view **B.** Frontal view **C.** Dorsal view. Images by Alex Wild.

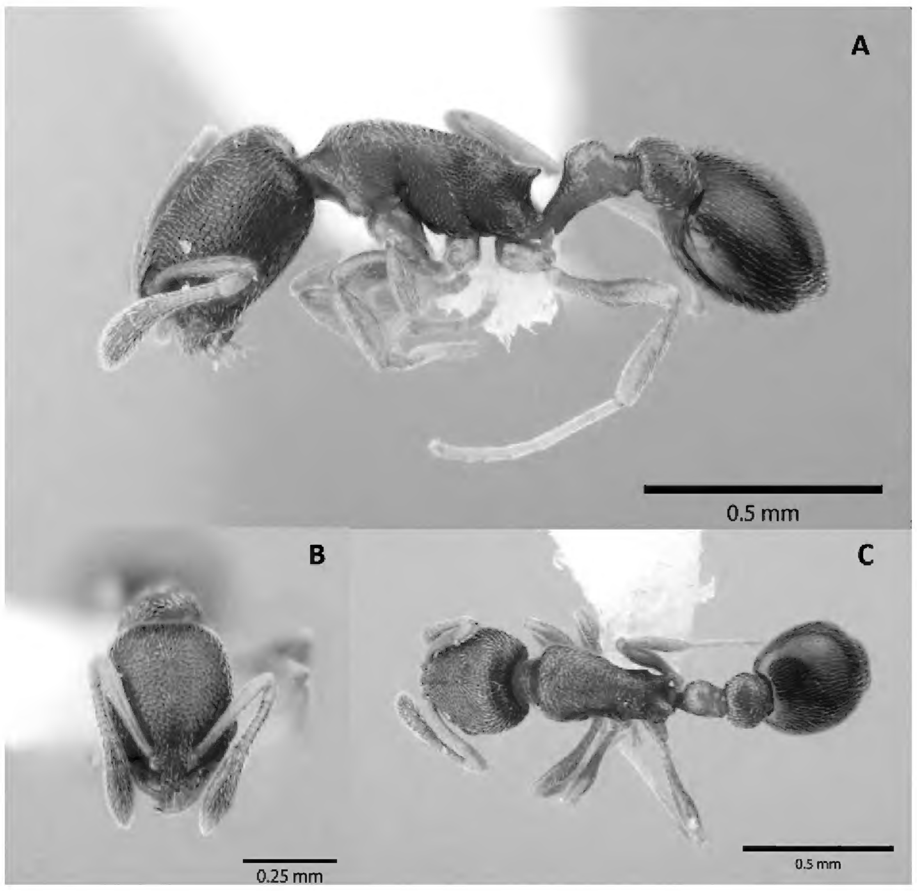

Figure 3. *Cardiocondyla minutior* (UTIC215115). **A.** Lateral view **B.** Frontal view **C.** Dorsal view. Images by Alex Wild.

***Cardiocondyla minutior* Forel, 1899**
Figures 3, 10c

Materials examined. ECUADOR – **Pichincha** • Quito, Mitad del Mundo; −00.0021, −078.4563; 2480 m alt.; 07.XII.2003; A. Wild & J. Vieira leg; active search; UTIC00215115.

Published records. **Orellana** • Dayuma, Santa Rosa; −00.671, −076.7005; 250 m alt.; 01.VII.2008; D. Donoso leg. (Donoso et al. 2014).

Identification. Head elongated, with straight to slightly concave occipital margin; postocular distance large; anterior clypeal margin concave medially; metanotal groove vestigial; body without rugae; propodeal spines short and acute; in dorsal view, petiolar node subcircular; in lateral view, postpetiolar node lower than petiolar node, with flat sternite (Seifert 2022).

Common name. Lesser Sneaking Ant

Comments. This species is pantropically distributed. Its populations prefer nesting in different habitats: from dry coastal forests to lowland rain forests. This species is possibly native to the Indo-Malayan region (Seifert 2003). However, Seifert (2022) pointed out that around 72% of all samples he studied came from the Caribbean region, as well as various islands of the Pacific, while only 16% are from the Indo-Malayan region.

The present records are from the Mitad del Mundo area; we collected specimens at a site surrounded by pastures used for grazing cattle. Seifert (2022) similarly reported this species from disturbed open areas, either with bare ground or scarce herbs. This species is omnivorous and apparently forms small colonies; according to Seifert (2022), these characteristics further coexistence with other tramp ants, even if *C. minutior*

is outnumbered; an example of co-occurring colonies is with *Linepithema humile*. Although its geographic distribution is expected to increase in the future, it seems unlikely that *C. minutior* will ever become a major dominant pest (Seifert 2022).

***Cardiocondyla wroughtonii* group**
Figures 4, 10c

Materials examined. ECUADOR – **Santo Domingo de Los Tsáchilas** • Santo Domingo, Luz de América, El Esfuerzo; −00.5142, −079.2999; 219 m alt.; 13.II.2022; A. Pazmiño, J. Salazar-Basurto leg.; Winkler extractor; MECN-EN-HYM 4301 – **Loja** • Catamayo, Alamala; −03.5914, −079.1153; 1231 m alt.; 01.V.2014; A. Castro leg.; active search; CISEC0005299.

Published records. ECUADOR – **Loja** • Catamayo, Alamala; −03.9860, −079.4259; 1628 m alt.; 12.XI.2013; A. Castro leg.; active search; PBA0394, PBA0665, PBA0659 • Macará, Canguraca; −04.210, −079.880; 933 m alt.; 2.X.2014; M. Tuza, M. Vélez, C. Gomez, G. Piedra, J. Lattke leg.; active search; BCCISEC0010125, BCCISEC0010124 (Donoso et al. 2014).

Identification. This species group can be identified by the following characters: head rather short with comparably low postocular index (CL/CW 1.099–1.189; PoOc/CL 0.415–0.440) and variably wide frons (FRS/CS 0.219–0.282); scape short to very short (SL/CS 0.682–0.825); metanotal depression well developed (MGr/CS 3.25–3.65%); propodeal spines rather short (SP/CS 0.184–0.201); postpetiole higher (PpH/CS 0.276–0.337) with bilobate or bicuspidate sternite (Seifert 2022). Within this group, *C. wroughtonii* and *C. obscurior* are considered worldwide tramp species. Seifert (2003) mentioned specimens which were previously identified as *C. wroughtonii* have been misidentified as *C. obscurior.* Due to the morphological complexity and small size, distinguishing these two species requires physical examination by specialists in the genus. Since these misidentifications occurred in South America (Dekoninck et al. 2019), we show below the information corresponding to both species. See details of morphometric indices by Seifert (2003).

Common name. Sneaking ants.

Comments. Species in the *C. wroughtonii* group are often associated with vegetation, usually nesting in hollowed out, decaying branches and plant cavities, such as grass stems. They are found in open areas, in grasslands, and at forest margins (Deyrup et al. 2000). In Valle del Cauca, Colombia, these species have been found in secondary forests and pastures in the same localities (Dekoninck et al. 2019). Our specimens were found using in Winkler sifter samples taken in areas with anthropic influence, specifically in the transition zones between melina (*Gmelina arborea*) plantations and native secondary rainforest at 219 m a.s.l. in Santo Domingo Province.

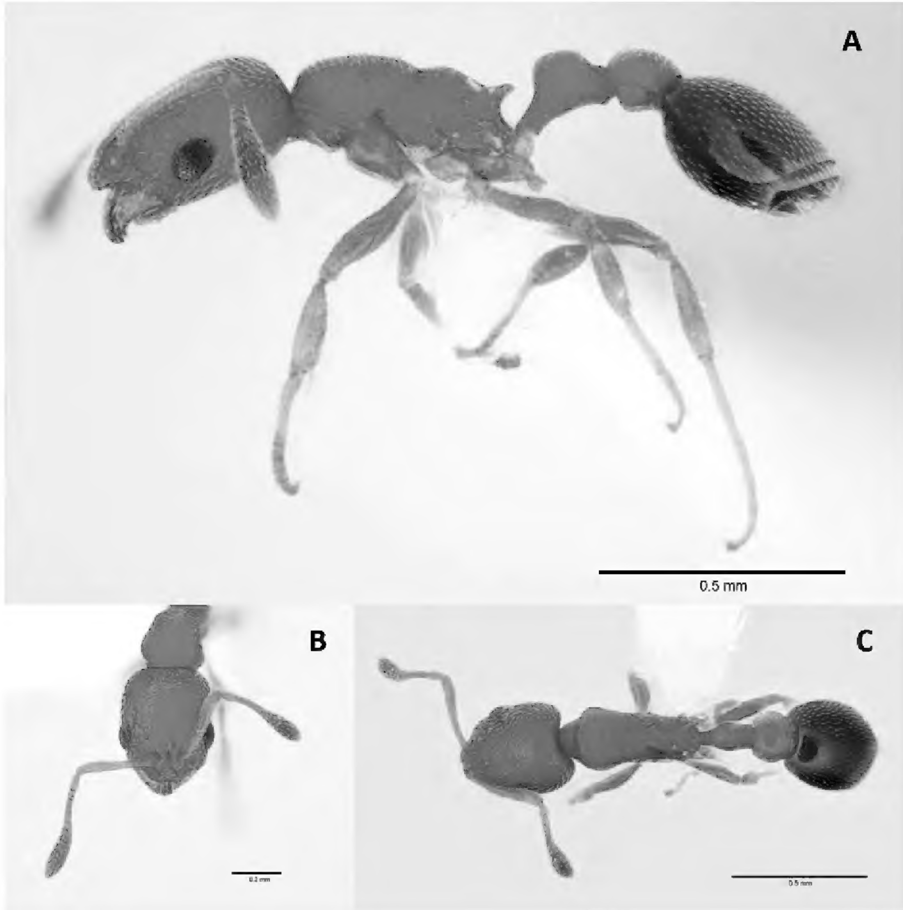

Figure 4. *Cardiocondyla wroughtoni* (CISEC0005299_P). **A.** Lateral view **B.** Frontal view **C.** Dorsal view. Images by Adrian Troya.

***Linepithema humile* (Mayr, 1868)**
Figure 10a

Materials examined. ECUADOR – **Pichincha** • Quito, Mitad del mundo; −00.002, −078.456; 2425 m alt.; 07.XII.2003; A. Wild, J. Vieira leg.; active search; UTIC215108 • Quito, Cotocollao; −00.1119, −078.495; 2758 m alt.; 01.III.2006; O. Acuña leg.; active search; MEPN31779, MEPN31780.

Published records. ECUADOR – **Pichincha** • Quito, Mitad del mundo; 00.000, −078.450; 2483 m alt.; 07.XII.2003;A.. Wild, J. Vieira leg.; active search; MCZ 560883 (Donoso et al. 2014) • Quito, Mariana de Jesús; −00.190, −078.494; 2732 m alt.; 01.X.2002; M. Salvador leg.; active search; CASENT0013479 (Antweb 2023) • Quito, Parque Arqueológico y Ecológico Rumipamba; −00.183, −078.500; 2732 m alt.; 18.I.2002; T. De Vries leg.; active search; CASENT0013537 (Antweb 2023) • Quito, Carapungo; −00.088, −078.449; 2600 m alt.; 30.XI.2003; A. Wild leg.; active search; CASENT0013634 (Antweb 2023) – **Imbabura** • Otavalo; 00.2410, −078.2478; 2549 m alt.; "kevin_perugachi" obs.; 10.IV.2022; iNaturalist observation (https://inaturalist.org/observations/111262036) – **Tungurahua** • Ambato; −01.2478, −078.6183; 2599 m alt.; "sofiadelatorreee" obs.; 09.XI.2020; active search; iNaturalist observation (https://inaturalist.org/observations/64641537) – **Azuay** • Cuenca, Padre Juan Arteta; −02.910, −079.033; 2580 m alt.; C. Criollo obs.; 08.XII.2020; active search; iNaturalist observation (https://doi.org/10.15468/ab3s5x) – **Orellana** • Parque Nacional Yasuní, Estación Científica Yasuní PUCE; −00.671, −076.400; 243 m alt.; C. Reyes-Puig, G. Ríos-Alvear leg.; active search (Reyes-Puig and Ríos-Alvear 2015).

Identification. Anterior portion of the metapleural gland orifice with moderately common to abundant

appressed hairs. Pronotum usually without erect setae, or rarely with one pair; length of maxillary palps half that or less than HL; metanotal groove slightly to moderately impressed; propodeum inclined anteriorly, with dorsal and posterior face forming an obtuse angle. Antennal scapes long, equal to or longer than HL; pronotum and first gastric tergite without setae; mesonotum straight, not angular or swollen (Wild 2004; Escárraga and Guerrero 2016).

Common name. Argentine Ant

Comments. This species is native to southern South America, including the countries of Argentina, Uruguay, Paraguay, and Chile. It has been introduced in many parts of the globe and is now considered as one of the 100 worst invasive species in the world (Lowe et al. 2000; Suárez et al. 2001). In Ecuador, we found records from Imbabura, Pichincha, Tungurahua and Azuay provinces. We were unable to verify the record of Reyes-Puig and Ríos-Alvear (2015) from the Amazonian province of Orellana due to the lack of vouchered specimens, and therefore we can neither deny nor affirm its presence in this region of the Amazon. Future research to confirm its presence there, as well as to understand the behavior and potential impacts of *L. humile* on local ecosystems.

Colonies of *L. humile* are commonly found in the city of Quito and adjacent valleys, usually in abundance, as well as in other Andean cities like Otavalo, Ambato, and Cuenca. We hypothesize this species is exclusively found in the human-modified highlands in Ecuador, a relatively large region known as the "Sierra", the settlement place for many urban and rural populations. According to Gordon et al. (2001), this species is very adaptable and can survive in a wide variety of environments, although mainly in temperate zones.

Linepithema humile can have a significant impact on native ant communities, as well as on other insects (Suarez and Case 2002). This species can outcompete many others for food and other resources, and it can alter the local ant community composition (Suarez and Case 2002). *Linepithema humile* can also negatively affect agriculture by damaging crops by feeding on roots and seeds and by protecting and carrying insect pests, which increase the incidence of crop diseases (Wild 2004). In the aforementioned Ecuadorian cities, populations of *L. humile* frequently invade properties, parks, and streets in urban and rural areas.

Monomorium floricola (Jerdon, 1851)

Figure 10d

Materials examined. ECUADOR – **Orellana** • San José de Payamino, Timburi Cocha Research Station; −00.4868, −077.2779; 312 m alt.; 09.II.2018; X. O'Reilly-Berkeley leg.; active search; MECN-EN-HYM 7371 • Dayuma, Santa Rosa; −00.6986, −076.7171; 290 m alt.; 16.VIII.2021; A. Pazmiño leg.; active search; MECN-EN-HYM 4995, MECN-EN-HYM 4996 • Aguarico, Tambococha; −00.9781, −075.4255; 194 m alt.; 02.IX.2021; A. Pazmiño leg.; active search; MECN-EN-HYM 4993, MECN-EN-HYM 4994 – **Guayas** • Guayaquil, Bosque Protector Cerro Blanco; −02.1441, −080.0855; 160 m alt.; 15.IV.2017; A. Pazmiño leg.; active search; CB_052.

Published records. – **Orellana** • Alejandro Labaka, Parque Nacional Yasuní, Estacion Cientifica Yasuní; −00.67, −076.400; 243 m alt.; 01.VIII. 2007; Donoso, D leg.; Z_002, HICD_E18 – **Sucumbíos** • Lago Agrio; 0.0866, −076.8911; 306 m alt.; 18.II.2021; J. Montalvo obs.; iNaturalist observation (https://www.inaturalist.org/observations/82243634) – **Esmeraldas** • Quinindé, Malimpia, Reserva Biológica Canandé; 00.5243, −079.2126; 265 m alt.; 21.IV.2018; P. Hoenle obs.; iNaturalist observation (https://www.inaturalist.org/observations/77640223) – **Manabí** • Manta, Lazareto; −00.9541, −080.7070; 0 m alt.; 10.VII.2021; C. Rodríguez-Moreira obs.; iNaturalist observation (https://www.inaturalist.org/observations/88077876) • Manta, Lazareto; −00.9541, −080.7071; 0 m alt.; 10.XI.2021; C. Rodríguez-Moreira obs.; iNaturalist observation (https://www.inaturalist.org/observations/100970387) • Manta, Lazareto; −00.9541, −080.7071; 0 m alt.; 17.IV.2021; C. Rodriguez-Moreira obs.; iNaturalist observation (https://www.inaturalist.org/observations/79891944) – **Morona Santiago** • Tiwintza, Palomino; −03.0358, −078.1031; 388 m alt.; 03.III.2019; Padrón, S.leg.; active search; MZUA-EN47226 to MZUA-EN47337 (Padrón et al. 2022).

Identification. Head width smaller than 0.35 mm; mesosoma pale yellow, strongly contrasting with darker head and gaster (Fernández 2007); in frontal view, head rectangular, dorsum flat, shiny, and smooth, bearing erect or semi-erect, long and short setae anteriorly; eyes elongate, placed midlength on head; antennae with 12 antenommeres, apically with 3-segmented club; promesonotum slightly rounded anteriorly; in lateral view, mesosoma slightly flattened posteriorly; metanotal groove well marked; propodeum smooth and shiny; propodeal spiracle without visible vestibule; in lateral view, petiole usually lacking ventral lobe, conical, and slightly taller than postpetiole (Heterick 2006).

Common name. Flower Ant

Comments. This species is native to Asia and has a wide distribution globally. It prefers disturbed tropical areas with anthropic influence. We found individuals in boats and stations of park rangers and military personnel at Yasuní National Park. These personnel use the boats to transport goods and tourists to parts of the reserve, so this might be the most probable means by which new colonies may be established. At another Amazonian locality, in San José de Payamino, we found colonies inside phytotelmata of bromeliads. We also found the first records of this species in the seasonally dry- and in the rain forests of the Chocó-Darién biome, part of the lowland tropical forests in northwestern Ecuador; we collected the specimens on shrubby vegetation from two natural reserves.

Monomorium floricola is one of the most widely

distributed tramp ants worldwide, and it can adapt to new habitats due to its varied biological attributes. For example, because queens lack wings and cannot disperse by flying, new colonies are formed through budding, which is when a part of a large colony which breaks off to form a new one (Snelling 2005).

***Monomorium pharaonis* (Linnaeus, 1758)**
Figures 5, 10d

Materials examined. ECUADOR – **Zamora Chinchipe** • Zamora, Posada Copalinga; −04.0911, −078.9621; 1060 m alt.; M. Tuza, G. Vélez, G. Gómez, G. Piedra, J. Lattke leg.; 25. X.2014; active search; ATPFOR2122.

Published records. – **Manabí** • Flavio Alfaro, La Crespa; −00.3356, −079.7587; 223 m alt.; V. Herrera obs.; 13.XII.2019; iNaturalist observation (https://www.inaturalist.org/observations/36656173) • Manta, Ciudad del Sol; −00.9625, −080.7558; 72 m alt.; D. Velasco obs.; 13.X.2021; iNaturalist observation (https://www.inaturalist.org/observations/98133980) – **Pichincha** • Quito; −00.199, −078.511; 2900 m alt.; G. Onore leg.; 13. VIII.2013 (Donoso et al. 2014) – **Orellana** • Parque Nacional Yasuní, Estación Cientifica Yasuní PUCE; −00.67, −076.400; 243 m alt.; D. Donoso leg.; 01.VIII.2007; active search; HICD_C1 (Donoso et al. 2014) • Dayuma, Santa Rosa; −00.671, −076.701; 250 m alt.; D. Donoso leg.; 01.VII.2008; active search (Donoso et al. 2014) – **Guayas** • Guayaquil, Cerro del Carmen; −02.18, −079.88; 8 m alt. (Fernandez and Sendoya 2004).

Identification. Head and mesosoma finely reticulate-punctate; mandibular dorsum with coarse longitudinal rugae; two rows of hairs between vertex and front carina (Fernández 2007); promesonotum convex with 2–6 setae; metanotal groove well marked; propodeum slightly rounded. The following is from Wetterer (2010b): head, mesosoma, petiole and post-petiole matte with varying yellowish tones, gaster with darker tones; body color may vary even within the same colony.

Common name. Pharaoh Ant

Comments. This species is generally found in tropical and temperate anthropized habitats (Bolton 1987). *Monomorium pharaonis* is possibly native to the Asian tropics since most records are found in this region, and these belong not only from human-populated areas but also from natural preserves (Wetterer 2010b). In Ecuador this species has been found at Yasuní National Park, in the Amazon region, but also in major cities, such as Quito. Donoso et al. (2014) observed that workers collected inside a Quito residence showed very aggressive behavior. We also collected specimens from domestic areas in Quito. In addition, our records from the province of Manabí are the first for the coastal lowland dry forests of western Ecuador; these specimens were observed inside buildings as well.

Fernández and Sendoya (2004) and Wetterer (2010b) cited records in the city of Guayaquil; however, these

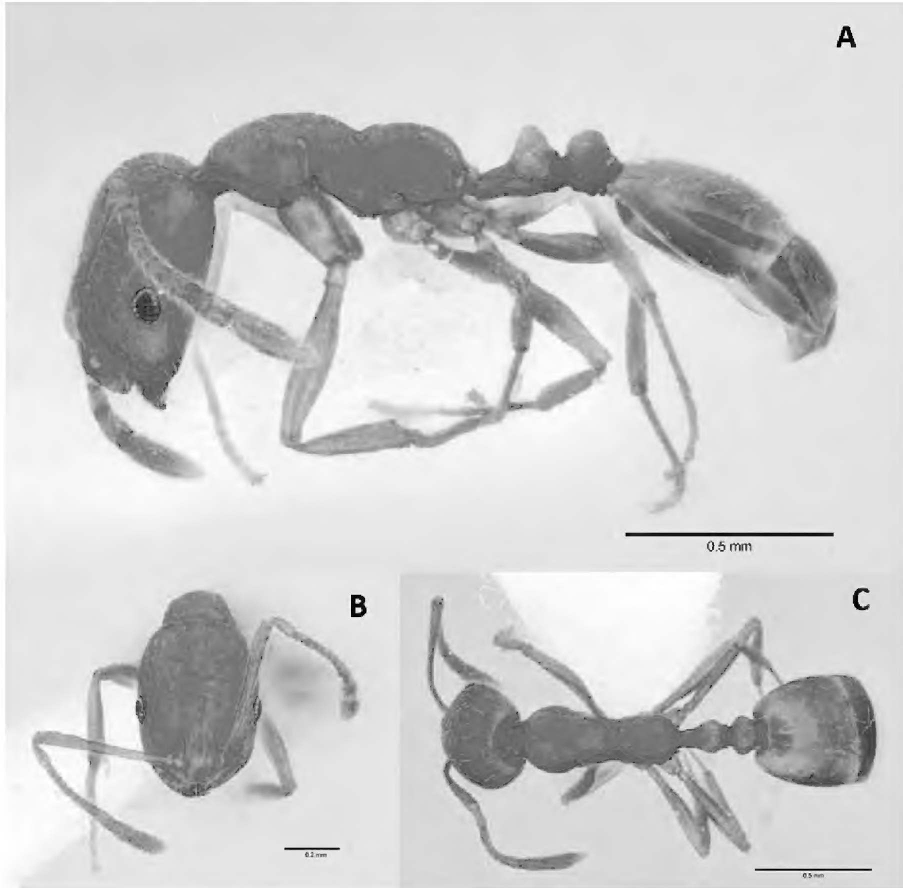

Figure 5. *Monomorium pharaonis* (ATPFOR2122). **A.** Lateral view **B.** Frontal view **C.** Dorsal view. Images by Adrian Troya.

are likely misidentifications, as previously noted by Donoso et al. (2014).

The success of this species is possibly due to the establishment of giant, polygynous, and polycalic colonies, which can reach several million individuals. Workers forage along crevices and scavenge from food sources like mammal corpses and dead insects (Abdar 2020). Due to their high density, they are hard to eradicate using, for example, fumigation with chemical-based insecticides; these ants can penetrate deep into the structures of buildings (Collingwood 1979).

***Nylanderia fulva* (Mayr, 1862)**
Figure 10a

Materials examined. ECUADOR – **Guayas** • Marcelino Maridueña, Ingenio San Carlos; −02.205, −079.484; 31 m alt.; 01.XII.2018;J. Mendoza leg.; active search; MECN-EN-HYM 3686 to MECN-EN-HYM 3689.

Identification. Workers can be separated from other closely related species by their reddish-brown to yellow body, relative eye index less than 30, and long mesosomal macrosetae (index of longest pronotal macrosetae/propodeum height at least 60). However, it is necessary to examine the pubescence of the male terminalia to separate *N. fulva* (sparse and uneven setae) and *N. pubens* (dense fringe of setae). Workers of both species are very similar morphologically (Sharma et al. 2015; LaPolla and Kallal 2019).

Common name. Tawny Crazy Ant

Comments. *Nylanderia fulva* is native to southern South America, and its presence in Ecuador was first reported in sugarcane crops in Guayas province by Pazmiño-Palomino et al. (2020), who reported a mutualistic association between the ants and the white aphid *Melanaphis sacchari* Zehntner. The sugarcane crops

were highly infested by the aphids, and Pazmiño-Palomino et al. (2020) hypothesized this to be caused by an association with the ants. Further research is required to get a fuller understanding of the ecological dynamics of the populations of *N. fulva* in Ecuador.

Nylanderia fulva is generally omnivorous and feeds on a wide range of sources, including dead insects, nectar, and fruits, and it may be associated with plant-sucking hemipterans. This species can also damage plants and crops and is known to interact aggressively with native ant species (Eyer et al. 2018).

***Paratrechina longicornis* (Latreille, 1802)**
Figure 10b

Materials examined. ECUADOR – **Sucumbíos** • Cuyabeno, Puente Cuyabeno; −00.0306, −076.3161; 244 m alt.; 09.VIII.2021; A. Pazmiño leg.; active search; MECN-EN-HYM 3716, MECN-EN-HYM 3717 • same locality; −00.0306, −076.3161; 244 m alt.; 08.VIII.2021; J. Salazar-Basurto leg.; tuna bait; MECN-EN-HYM 3718, MECN-EN-HYM 3719 – **Orellana** • Aguarico, Tambococha; −00.9781, −075.4255; 194 m alt.; 03.IX.2021; A. Pazmiño, J. Salazar-Basurto leg.; active search; MECN-EN-HYM 2556 • Aguarico, Río Cononaco; −01.0100, −076.3800; 245 m alt.; 01.X.1988; J. Valarezo leg.; active search; MECN-EN-HYM 3715 – **Imbabura** • San Miguel de Urcuquí, Termas de Chachimbiro; 00.4676, −078.2800; 2348 m alt.; 05.IV.1988; D. Bastidas; active search; MECN-EN-HYM 3690 to MECN-EN-HYM 3705, MECN-EN-HYM 3710 to MECN-EN-HYM 3713 • Ibarra, El Juncal; 00.4320, −077.9650; 1960 m alt.; 06.IV.1988; D. Bastidas leg.; active search; MECN-EN-HYM 3706 to MECN-EN-HYM 3709.

Published records. ECUADOR – **Napo** • Tena, Paushiyacu; −00.9918, −077.8143; 532 m alt.; 26.IV.2019; A. Pazmiño obs.; iNaturalist observation (https://www.inaturalist.org/observations/23744434) – **Santo Domingo de los Tsáchilas** • Santo Domingo, Parque La Madre; −00.2561, −079.1805; 516 m alt.; 08.XII.2019; P. Flores obs.; iNaturalist observation (https://www.inaturalist.org/observations/36240141) • Santo Domingo , Río Toachi; −00.2561, −079.1269; 574 m; 29.XI.2019; A. del Pozo; iNaturalist observation (https://www.inaturalist.org/observations/36487696) – **Guayas** • Guayaquil, Puná; −02.5618, −080.0871; 0 m alt.; 07.VII.2021; G. Quijije obs.; iNaturalist observation (https://www.inaturalist.org/observations/86120247) • Guayaquil, El Fortín; −02.1080, −079.9510; 17 m alt.; I.XI.2020; D. Tábara obs.; iNaturalist observation (https://www.inaturalist.org/observations/64131300) • Guayaquil, Calle 54; −02.1707, −079.4698; 30 m alt.; 09.XI.2020; J. Mendoza obs.; iNaturalist observation (https://www.inaturalist.org/observations/64652647) • Guayaquil, Isaías; −02.1251, −079.9374; 33 m alt.; 25.IV.2020; A. Pazmiño obs.; iNaturalist observation (https://www.inaturalist.org/observations/43477125) • Durán, Vía San Jacinto de Yaguachi; −02.1855, −079.8045; 4 m alt.; 21.XII.2020; J. Criollo obs.; iNaturalist observation (https://www.inaturalist.org/observations/66895835) – **Loja** • Zapotillo, La Ceiba; −04.3098, −080.2150; 233 m alt.; 26.IV.2022; "tjar" obs.; iNaturalist observation (https://www.inaturalist.org/observations/43837474) – **Santa Elena** • Salinas, La Libertad; −02.2401, −080.9160; 24 m alt.; 06.XI.2020; S. Zambrano obs.; iNaturalist observation (https://www.inaturalist.org/observations/64336784) • Salinas, San Francisco; −02.2237, −080.9200; 7 m alt.; 10.XI.2020; E. Cisneros obs.; iNaturalist observation (https://www.inaturalist.org/observations/64665291) – **Sucumbíos** • Nueva Loja, Cascales; 00.0881, −076.9011; 306 m alt.; 02.II.2021; "lisseth123" obs.; iNaturalist observation (https://www.inaturalist.org/observations/68978589) – **Manabí** • Manta, Ciudad Sol; −00.9617, −080.7552; 71 m alt.; 16.XI.2021; D. Velasco obs.; iNaturalist observation (https://www.inaturalist.org/observations/101342872) • Portoviejo, Areopuerto Reales Tamarindos; −01.0430, −080.4797; 43 m alt.; 02.X.2020; G. Intriago obs.; iNaturalist observation (https://www.inaturalist.org/observations/62309668) – **Zamora Chinchipe** • Tundayme; −03.6282, −078.5890; 925 m alt.; 18.VI.2021; "chinoh3" obs.; iNaturalist observation (https://www.inaturalist.org/observations/83890175) – **Los Ríos** • Buena Fe, Centro Científico Río Palenque; −00.5880, −079.3630; 170 m alt.; 1976; J. Peck leg.; Museum of Comparative Zoology, Harvard University (Wetterer 2008; James Wetterer's unpublished data) – **El Oro** • Machala, Jubones; −03.25, −079.95; 8 m alt.; 1981; J. Escobar; Smithsonian National Museum of Natural History (Wetterer 2008; James Wetterer's unpublished data).

Identification. Manbibles mostly with five teeth (only *P. kohli* has eight teeth); head narrow, clearly longer than broad, with abundant erect macrosetae; scapes without erect macrosetae; eyes large and convex, breaking lateral head margin in frontal view; mesosoma with scattered, pale, erect macrosetae; pronotum and mesonotum almost flat dorsally; propodeum nearly flat to slightly domed posteriorly; gaster with abundant, pale, erect macrosetae (LaPolla and Fisher 2014).

Common name. Longhorn Crazy Ant

Comments. This species is probably native to Asia (Sharaf et al. 2017) and is usually found in disturbed temperate, tropical, and subtropical habitats around the world (Wetterer 2008). However, it also has been detected in less-disturbed or even well-preserved areas, such as in the southern region of Yasuní National Park (A. Troya pers. obs. 2002). It has been previously recorded in continental Ecuador by Wetterer (2008). We provide new records of this species in tropical lowland, urban areas on both sides of the Andes; these records come from highly disturbed habitats, mainly associated with agriculture and cattle-ranching, and a number of these records are of colonies living in households or from public areas like streets and parks. We also report this species from the Reserva de Producción de Fauna Cuyabeno in northern Ecuadorian Amazonia. We hypothesize that *P. longicornis* possibly reached this reserve

with tourists, since we collected specimens around the Park Ranger Station of the reserve, the access site for all visitors, and we also found *P. longicornis* workers in the lodging area within the reserve. However, we did not find specimens in the forest, for example, along the trails.

Pheidole megacephala **(Fabricius, 1793)**
Figures 6, 7, 10e

Materials examined. ECUADOR – **Guayas** • Guayaquil, Jardín Botánico; −02.0798, −079.9088; 53 m alt.; 01. VIII .2016; H. Herrera leg.; active search; ATPFOR2119 – **Imbabura** • Valle del Chota; 00.3768, −078.0146; 2277 m alt.; 15.XI.2009; A. Troya leg.; pitfall trap [MEPN 35496 to MEPN 35505) – **Pichincha** • Quito; −00.1133, −078.4947; 2764 m alt.; 1.VII. 2015; A. Troya leg; active search (MEPN 35177 to MEPN 35180) • same locality; 1.III.2016; A. Troya leg; active search (MEPN: 37431) • Quito; −00.0975, −078.4222. 2682 m alt.; 1.VII.2015; A. Troya leg; active search (MEPN 35176 to MEPN 35180) • 1.III.2016. A. Troya leg; active search (MEPN 37432, MEPN 37433, MEPN 37434) • Quito, San Antonio, San Sebastian; −00.0161, −078.460, 2700 m alt, 01.VII.2022; O. Suing leg; active search (MECN-EN-HYM 7353 to MECN-EN-HYM 7355) • Quito, Tumbaco; −00.215, −078.411; 2332 m; 07.IV.2022; J. Salazar-Basurto leg; active search (MECN-EN-HYM 7366 to MECN-EN-HYM 7370).

Identification. In frontal view, head of major workers shiny, cordate-shaped, with rugae anteriorly; head of minor workers wider than long, mostly smooth and shiny; internal hypostomal teeth indistinct or absent; in lateral view, major workers with distinct dome on promesonotum, circular mesonotum, and oval postpetiole; first gastral tergite with scattered hairs (Fischer and Fisher 2013; Sarnat et al. 2015; Salata and Fisher 2022).

Common name. African Big-headed Ant

Comments. Non-native populations are found mainly in humid environments in close association with humans (Vanderwoude et al. 2000). This species is pantropical (Wilson 2003) and is considered among the five most destructive tramp ants in the world, but also among the 100 worst invasive species (Lowe et al. 2000). Its global spread has been associated with human trade (Wetterer 2012). In the Neotropics, it has been found mainly in urban areas, including isolated oceanic islands such as the Galapagos (Herrera et al. 2021) and Hawaii (Wetterer 2012).

In Ecuador this species has been found in the two large cities of Guayaquil and Quito, but also in one of the last remnants of Andean dry forests in the country, in the province of Imbabura (Troya et al. 2016); populations are still apparently small in Imbabura, as compared to others of the native myrmecofauna (A. Troya pers. obs. 2014).

Prior to our study, Ecuador was the only country in northern South America to lack confirmed records of this species. The specimens collected in the city of Quito exceed the altitudinal limit previously held for the species, which was, 2764 m a.s.l. (Al-Ameri et al. 2020). *Pheidole megacephala* preferentially preys on eggs and larvae of flies (Al-Ameri et al. 2020).

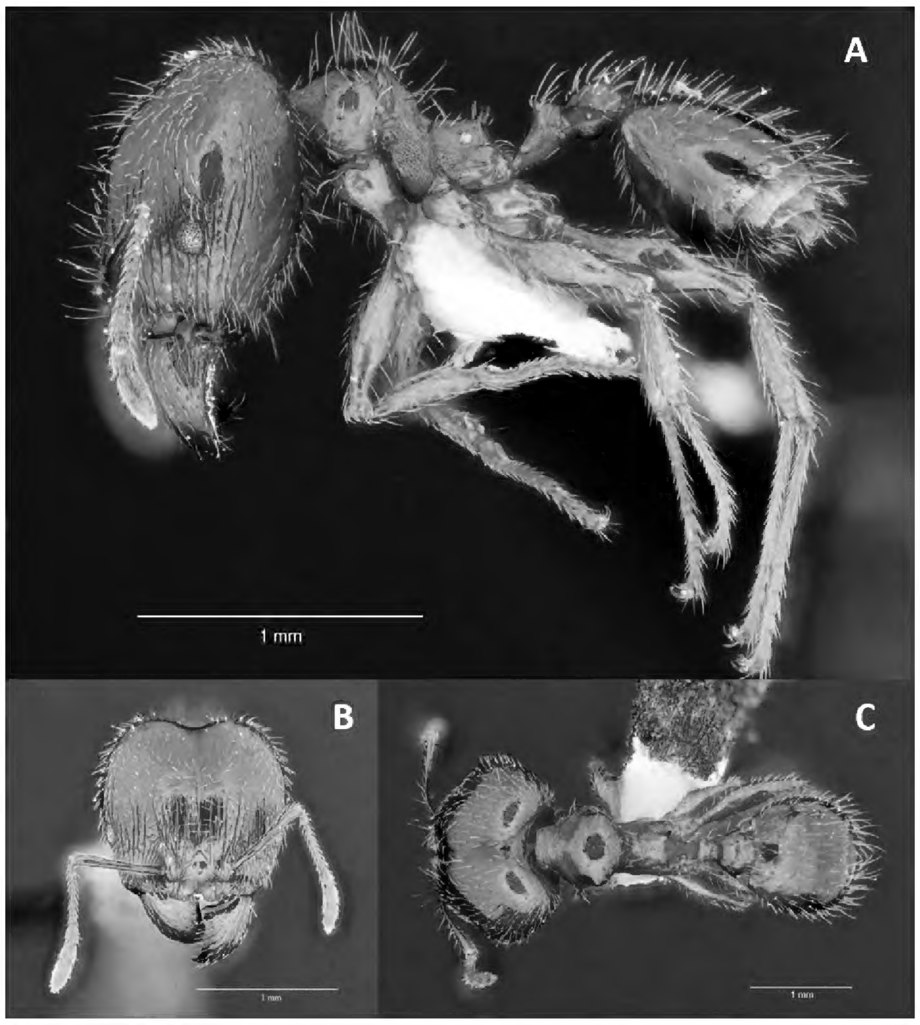

Figure 6. *Pheidole megacephala* (MEPN35497), major worker. **A.** Lateral view **B.** Frontal view **C.** Dorsal view. Images by Adrian Troya.

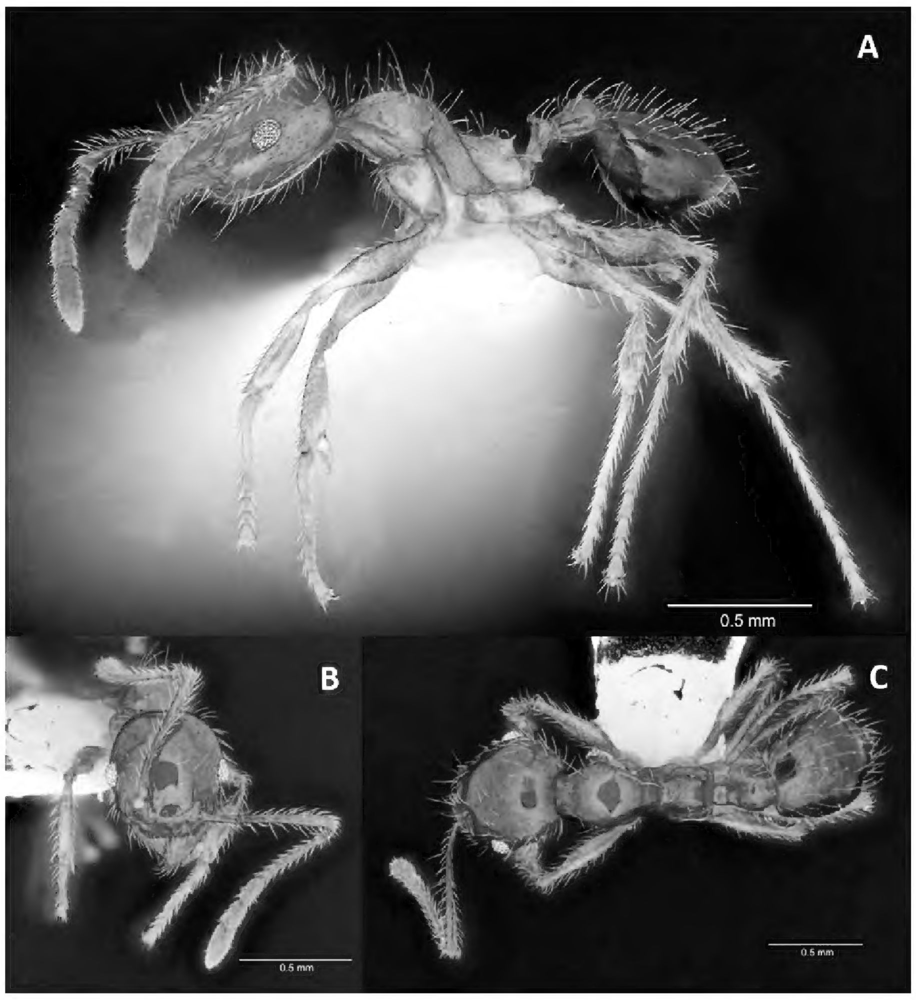

Figure 7. *Pheidole megacephala* (MEPN35505), minor worker. **A.** Lateral view **B.** Frontal view **C.** Dorsal view. Images by Adrian Troya.

Tapinoma melanocephalum (Fabricius, 1793)
Figure 10a

Materials examined. ECUADOR – **Guayas** • Guayaquil. Bosque Protector Cerro Blanco; 02.17268, 80.0221;

160 m alt.; 15. IV. 2017; A. Pazmiño leg.; active search; CB_036 – **Orellana** • Francisco de Orellana, Dayuma, Santa Rosa Yasuní; −00.703, −076.709; 290 m alt.; 15.VIII.2021. A. Pazmiño, J. Salazar-Basurto leg.; active search; MECN-EN-HYM 2549 • Francisco de Orellana, Dayuma, Parque Nacional Yasuní, Guardianía Pindo; −00.703, −076.709; 290 m alt.; 17.VIII.2021. A. Pazmiño, J. Salazar-Basurto leg.; active search; MECN-EN-HYM 2691, MECN-EN-HYM 2692 •Aguarico, Tambococha; −00.978, −075.426; 194 m alt.; 01. IX. 2021; A. Pazmiño, J. Salazar-Basurto leg.; active search; MECN: 2554 • Aguarico, Alejandro Labaka, Guardianía Añangu; −00.525, −076.387; 203 m alt.; 06. IX. 2021; A. Pazmiño, J. Salazar-Basurto leg.; active search; MECN-EN-HYM 2558, MECN-EN-HYM 7372 to MECN-EN-HYM 7374 • Aguarico, Nuevo Rocafuerte; −00.919, −075.404; 198 m alt.; 31.VIII.2021; J. Salazar-Basurto, A. Pazmiño leg.; active search; MECN-EN-HYM 2551 • **Sucumbíos**, Shushufindi, Limoncocha, Puerto Providencia; −00.462, −076.493; 223 m alt.; 06. IX. 2021; J. Salazar-Basurto, A. Pazmiño leg.; active search; MECN-EN-HYM 2552 • Sucumbíos, Shushufindi, Limoncocha, Palmeras del Ecuador; −00.291, −076.647; 265 m alt.; 07. IX. 2021; J. Salazar-Basurto, A. Pazmiño leg.; active search; MECN-EN-HYM 2553 • Sucumbíos, Cuaybeno, Aguas Negras, Nicky Amazon Lodge; −00.0692, −076.1636; 235 m alt.; 08.VI.2022; A. Pazmiño leg.; active search; MECN-EN-HYM 7356 to MECN-EN-HYM 7359).

Published records. ECUADOR – **Guayas** • Guayaquil, Puerto El Morro; −02.6113, −080.3041; 6 m alt.; 13.IX.2020; A. Icaza obs. (https://www.inaturalist.org/observations/59514854) – **Pichincha** • Puerto Quito, San Pedro de la Sucia, Calacalí–La Independencia road; 00.123, −079.247; 202 m alt.; 23.I.2020; A. Pazmiño obs. (https://www.inaturalist.org/observations/40323975) – Napo • Tena, Parque Amazónico Isla del Amor; −00.99355, −077.81522; 532 m alt.; 27.IV.2019; J.W. Cabrera Pino obs. (https://www.inaturalist.org/observations/23416696) • Tena, Casco Urbano; −00.9937, −077.8149; 532 m alt.; 27.IV.2019; J.W. Cabrera Pino obs. (https://www.inaturalist.org/observations/23416984) • Tena, Casco Urbano; −00.99263333, −077.807945; 532 m alt.; 24.IX.2020; M. Gallo obs. (https://www.inaturalist.org/observations/60788284) – **Esmeraldas** • Atacames; 00.8470, −079.9259; 0 m alt.; 04. V. 2019; R. Vallejo obs. (https://www.inaturalist.org/observations/24519853) • Atacames, Casa Blanca Club, 00.850, −079.921; 0 m alt.; 01.III.2021; D. Díaz obs. (https://www.inaturalist.org/observations/67816124) – **Manabí** • Flavio Alfaro; −00.3361, −079.7581; 15.XI.2019; V. Herrera obs. (https://www.inaturalist.org/observations/35721394) • Puerto López; −01.552, −080.811; 0 m alt.; 01. I. 2023; J. Salazar-Basurto obs. (https://www.inaturalist.org/observations/145610910) – **Pastaza** • Puyo; −01.4782, −078.0035; 1032 m alt.; 07.VII.2020; H. Velasteguí obs. (https://www.inaturalist.org/observations/52320675) • Mera, Shell; −01.5036, −078.0623; 1005 m alt.; 14. IX.2020; M. López obs. (https://www.inaturalist.org/observations/59743897) – **Zamora Chinchipe** • Zamora; −04.0662, −078.9502; 999 m alt.; 26.IX.2020; J. Montaño obs. (https://www.inaturalist.org/observations/60838833) – **Orellana** • Tiputini; −00.6015, −076.0985; 232 m alt.; 20.XII.2009; M. Mejía obs. (https://www.inaturalist.org/observations/41926716) • Francisco de Orellana, Yasuní National Park, Yasuní Scientific Station; −00.682, −076.400; 240 m alt.; 02.XII.2018; D. Forrister leg; active search; J. Longino collection jtlsv04121.02 (Antweb 2023) • Francisco de Orellana, Yasuní National Park, Yasuní Scientific Station; −00.670, −076.400; 243 m alt.; 03.I.2018; D. Donoso leg; active search (Antweb 2023).

Identification. Head ovoid, longer than wide; masticatory margin of mandible with conspicuous apical and subapical tooth, sometimes with relatively large third tooth; segments 3 and 4 of maxillary palps spatulate; head and mesosoma dark to light brown, metasoma light brown or pale yellow, almost transparent; legs yellowish, sometimes hyaline; maxillary palp elongate; fifth segment conical to slightly cylindrical, inserting ventrally on distal end of fourth segment (Guerrero 2018; Guerrero unpubl. data).

Common name. Ghost Ant

Comments. *Tapinoma melanocephalum* is possibly native to the Indo-Pacific region, but it now occurs throughout tropical, subtropical, and temperate areas of the world, where it has became a household pest. It is also commonly found in restaurants, hospitals, and greenhouses, and it is always associated with human activities (Wetterer 2009a). It has been previously recorded in Ecuador in Yasuní National Park (Donoso et al. 2014) and Macará, Loja (Lattke et al. 2016). We now record this species from urban areas and lowland tropical forests on both sides of the Andes, and in habitats with varying levels of human disturbance. In cities we found this species inside residential houses and other buildings. We also collected litter specimens in the buffer zone of a coastal, seasonally dry forest reserve. All our urban records are associated with food outlet sites in both Amazonian and coastal regions. In the coastal town of Puerto López, Manabí province, we collected workers of *T. melanocephalum* near the seashore; these ants were attracted to tomato leftovers.

***Tetramorium bicarinatum* (Nylander, 1846)**

Figures 8, 10e

Materials examined. ECUADOR – **Pichincha** • Quito, Iñaquito; −00.1772, −078.4784; 2700 m alt.; A. Troya leg.; 15.VII.2010; active search; MEPN 5526, MEPN 5527 – **Orellana** • Francisco de Orellana, Dayuma, Santa Rosa Yasuní Guardianship; −00.703, −076.709; 235 m alt.; 15.VIII.2021; A. Pazmiño, J. Salazar-Basurto leg.; active search; MECN-EN-HYM 2548 • Francisco de Orellana, Loreto, San José de Payamino; −00.4793, −077.2918; 315 m alt.; 28.VII.2018; X. O'Reilly leg; active search; MECN-EN-HYM 7351, MECN-EN-HYM 7352 – **Sucumbios** • Shushufindi, Limoncocha,

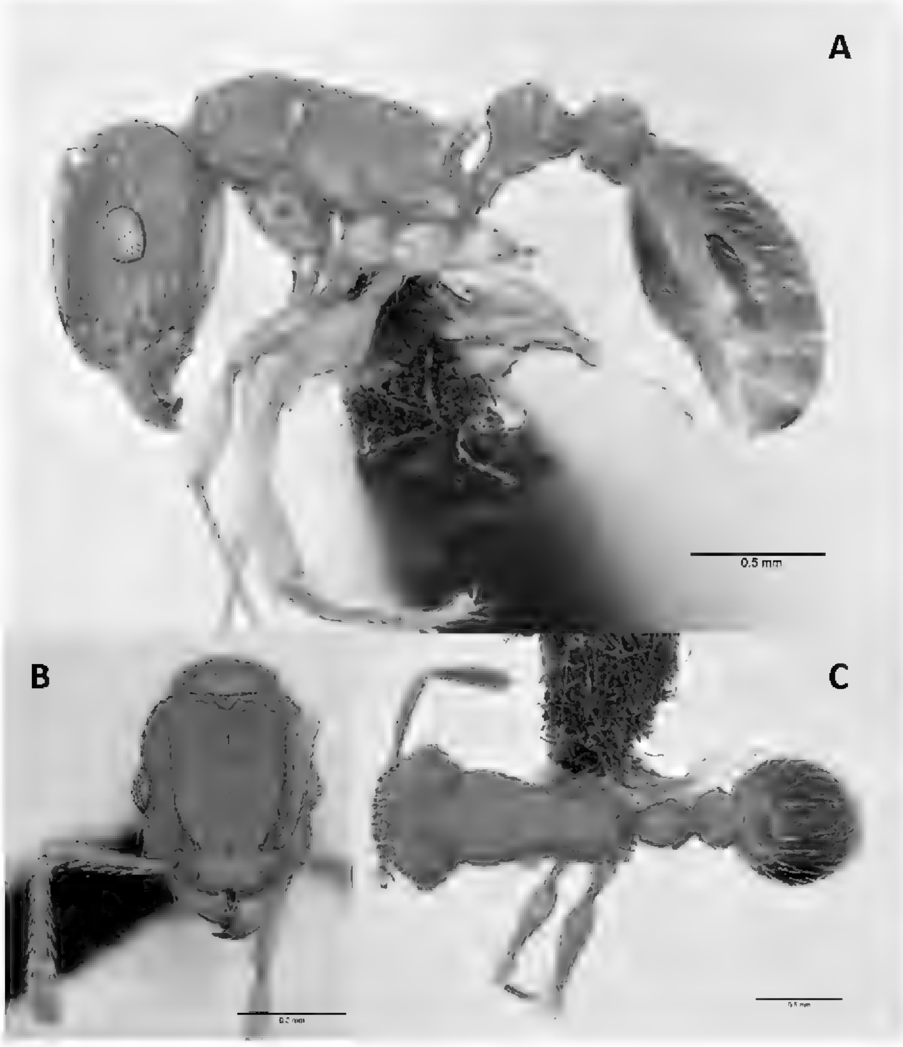

Figure 8. *Tetramorium bicarinatum* (MEPN 5527). **A.** Lateral view **B.** Frontal view **C.** Dorsal view. Images by Adrian Troya.

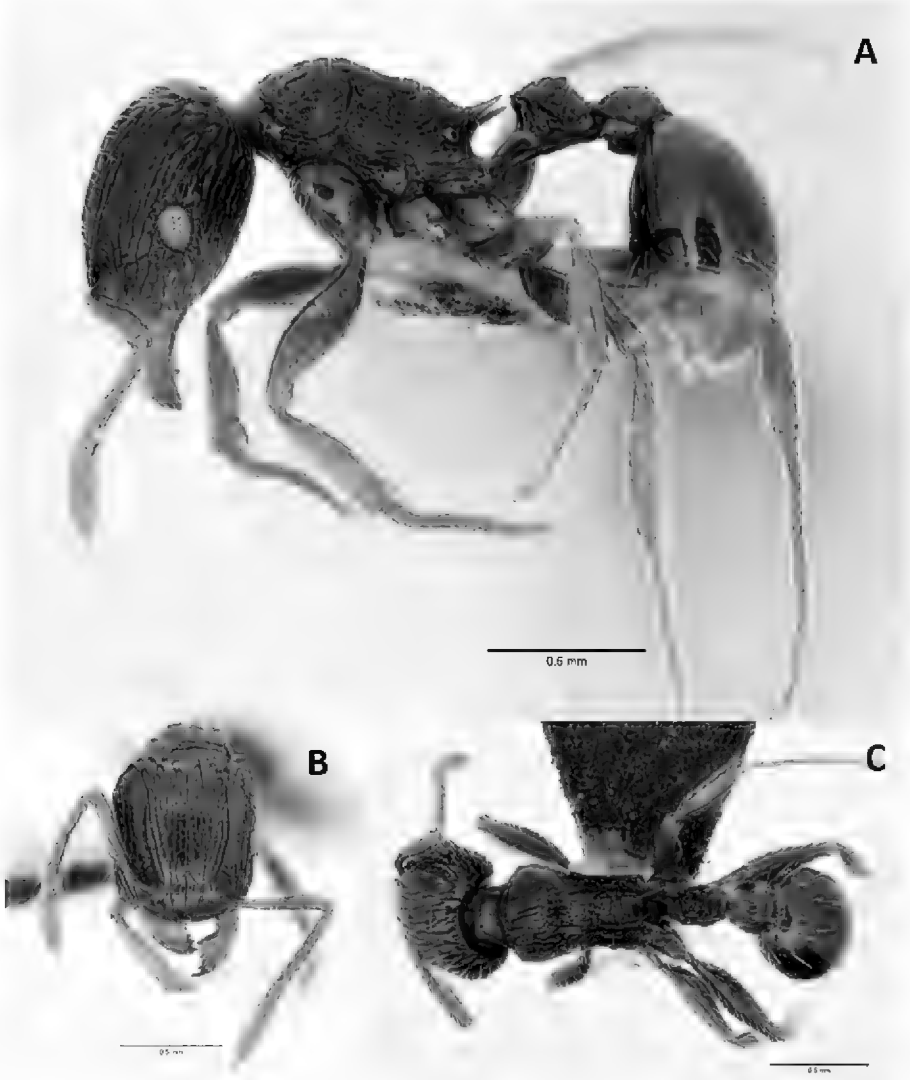

Figure 9. *Tetramorium lucayanum* (DS086). **A.** Lateral view **B.** Frontal view **C.** Dorsal view. Images by Adrian Troya.

Puerto Providencia; −00.462, −076.493; 223 m alt.; 06. IX. 2021; A. Pazmiño, J. Salazar-Basurto leg.; active search; MECN-EN-HYM 2557, 7360, & 7361 • Shushufindi, Limoncocha. Limoncocha, Community Reserve Limit; −00.386, −076.612; 240 m alt.; 12. IX. 2021; A. Pazmiño, J. Salazar-Basurto; active search; MECN-EN-HYM 2547.

Published records. ECUADOR – **Orellana** • Yasuní National Park, Yasuní Scientific Station; −00.675, −076.398; 240 m alt.; 06.III.2019 & 24.II.2020; D. Forrister leg; active search; J. Longino collection (jtl-sv04318.03, jtl-sv04364.05) (Antweb 2023) • Yasuní National Park, Yasuní Scientific Station; −00.670, −076.400; 243 m alt.; 01.VIII.2007 & 01.III.2015; D. Donoso leg; active search; HICD_E19, AMI_097, Z_003, KY_6_01_13_3 (Antweb 2023).

Identification. Minor workers: head elongate, with longitudinal irregular striae, posteriorly rugoreticulate, with well-defined frontal carinae; mandibles finely striate; scapes not reaching posterior head margin, when pulled posterad; metanotal groove mostly absent; propodeal spines medium-length to long relative to length of petiolar node in lateral view; petiolar node block-shaped; head, mesosoma, and petioles yellowish; gastral first segment mostly black (García and Fisher pers. obs. 2011).

Common name. Penny Ant

Comments. This species is found in the tropics and subtropics but also commonly occurs in temperate zones, mostly in disturbed areas. Nests may be found in warm artificial spaces, but this species also occurs in natural environments of oceanic islands for example (García and Fisher 2011). It has been collected from sea level to about 1600 m a.s.l. (AntWeb 2023). In Ecuador we collected specimens at a bar club in the city of Quito; this record is at about 2800 m a.s.l. and is the highest-known record for this species. Other records are from Otongachi Reserve in southwestern Pichincha province, at 850 m a.s.l., and from the Sucumbíos province in anthropized areas of the Amazon at 250 m a.s.l.

Tetramorium lucayanum Wheeler, 1905

Figures 9, 10f

Materials examined. ECUADOR – **Santo Domingo de Los Tsáchilas** • Otongachi; −00.314, −078.954; 850 m alt.; D. Donoso leg.; I.2015; MEPN Winkler (DS086).

Identification. Head with longitudinal, relatively broadly spaced rugulae, without dorsal cross-meshes; postpetiolar surface with broadly spaced, longitudinal rugulae (Bolton 1980).

Common name. Ebony Ant

Comments. According to Bolton (1980), this species belongs to the *T. lucayanum* complex, which is placed in the *T. camerunense* group. All four species of the *T. lucayanum* complex have rugae on the dorsal surface of the head, mesosoma, and petioles. *Tetramorium lucayanum* is very similar to *T. versiculum* but can be distinguished from the latter in showing relatively spaced, cephalic longitudinal striae without dorsal cross-meshes, whereas the cephalic striae are narrower and with some cross-meshes in *T. versiculum* (Bolton 1980). This species is widely distributed in sub-Saharan West Africa. It is also anthropogenically spread to the New World, including islands in the Caribbean: Cuba, Puerto Rico, Jamaica, the Virgin Islands, and the Bahamas

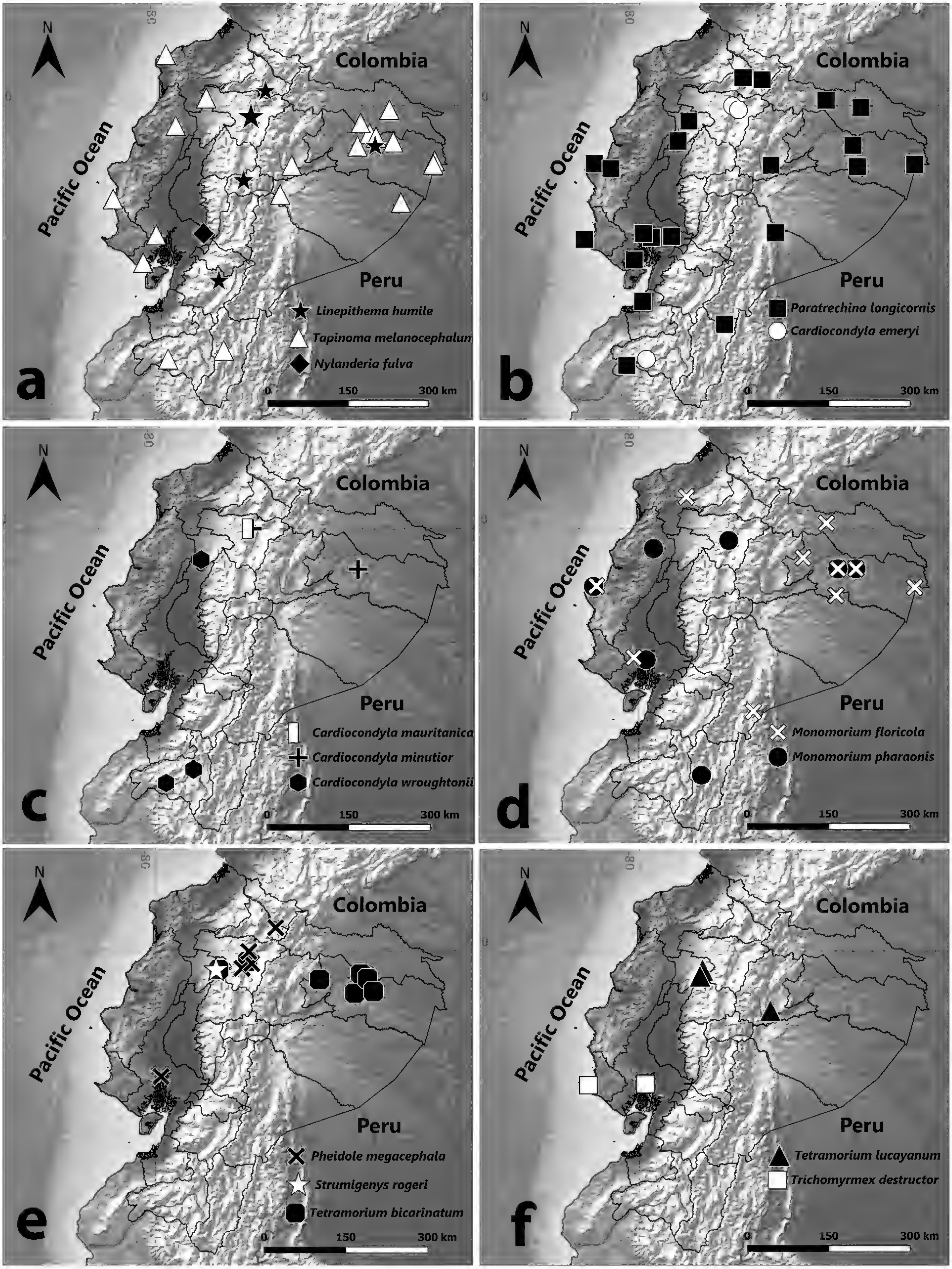

Figure 10. Records of all invasive ant species in continental Ecuador listed in Table 1. **a.** *Linepithema humile, Tapinoma melanocephalum, Nylanderia fulva.* **b.** *Paratrechina longicornis, Cardiocondyla emeryi.* **c.** *Cardiocondyla mauritanica, Cardiocondyla minutior, Cardiocondyla wroughttonii.* **d.** *Monomorium floricola, Monomorium pharaonis.* **e.** *Pheidole megacephala, Strumigenys rogeri, Tetramorium bicarinatum.* **f.** *Tetramorium lucayanum, Trichomyrmex destructor.*

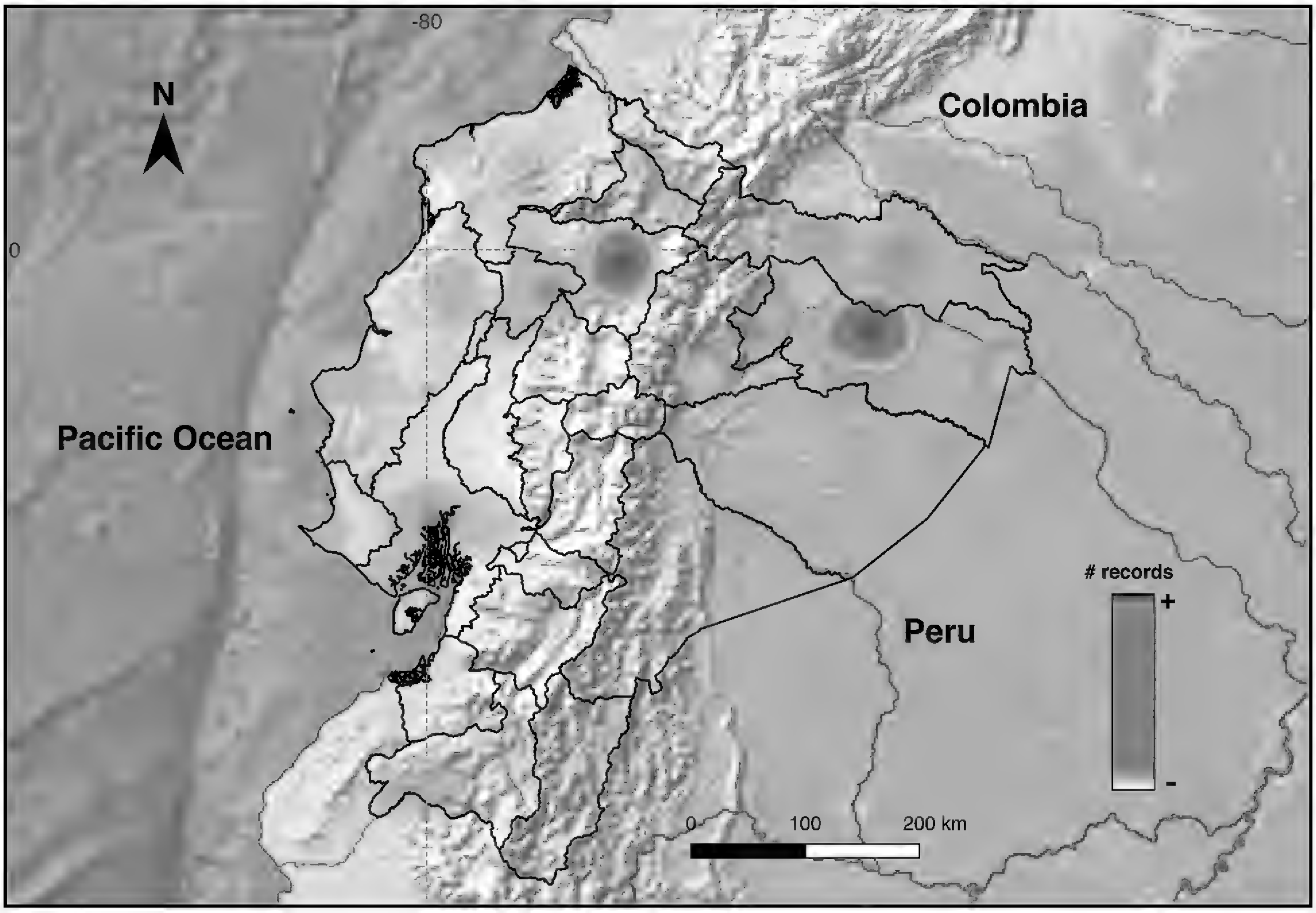

Figure 11. Distribution of presently examined tramp-ant species records in Ecuador. Heat regions (darker areas), represent those with higher frequency of records. Refer to the methodology for map construction details.

(Bolton 1980). Donoso et al. (2014) reported this species in Otongachi, a secondary, well-preserved forest in northwestern Ecuador, just 20 km east from a major town, Santo Domingo de Los Tsáchilas. Donoso et al. (2014) also commented that *T. lucayanum* may not negatively impact the native ant community at Otongachi, since they only found two specimens after long-term sampling in the reserve.

Discussion

We present the most complete compilation of records of exotic ant species with potentially established populations in continental Ecuador. Donoso et al. (2014) published the first list of tramp ants introduced to the country and listed 10 species. We add two species in our study: *Pheidole megacephala*, which is considered among the top insect pests in the world (Lowe et al. 2000), and *Cardiocondyla mauritanica*, which has not been recorded from South America before. We also add new site records for nine species: *Cardiocondyla emeryi*, *C. minutior*, *C. wroughtonii*, *Linepithema humile*, *Monomorium floricola*, *M. pharaonis*, *Paratrechina longicornis*, *Tapinoma melanocephalum*, and *Tetramorium bicarinatum*.

Considering the previous records of species by Wetterer (2009b), Domínguez et al. (2016), Lattke et al. (2016), and Pazmiño-Palomino et al. (2020), the total number of tramp ant species for the country is 15 (Table 1). This number is relatively high compared to neighboring countries, like Peru and Colombia. Eight tramp ant species are shared with Peru (nine are reported from that country; Bezděčková et al. 2015; Guénard and Economo 2015). Thirteen species are shared with Colombia (approximately 23 are reported there; Dekoninck et al. 2019). However, we consider that the number of species in Ecuador and neighboring countries may be biased due to different sampling efforts, as noted by Dekoninck et al. (2019). Based on our field experience in sampling ants at numerous sites and different habitats in Ecuador (Fig. 10), we suggest that current knowledge of exotic ant species in Ecuador is just emerging. Therefore, as previously suggested in other studies, any unexplored or poorly sampled habitat or ecosystem in this country can potentially yield important new data on the distribution of these insects (Pazmino-Palomino and Troya 2022).

Our results suggest many regions across Ecuador, particularly those having intensified human development, such as cities along the Andean mountains, large infrastructure projects, and monocultures, may have greater numbers of invasive ant species than other regions without human intervention. The heatmap in Figure 11 highlights the regions for which most records of invasive ants have been reported. Two of these regions, in the provinces of Pichincha and Orellana, show the highest concentration of records. In both provinces, commercial activities and tourism are

Table 1. Checklist of exotic ants in continental Ecuador. Provinces: AZ = Azuay; CO = Cotopaxi; ES = Esmeraldas; EO = El Oro; GU = Guayas; IM = Imbabura; LO = Loja; LR = Los Ríos; MA = Manabí; MS = Morona Santiago; NA = Napo; OR = Orellana; PA = Pastaza; PI = Pichincha; SE = Santa Elena; SD = Santo Domingo; SU = Sucumbíos; TU = Tungurahua; ZC = Zamora Chinchipe.

Number	Species	Provinces	References
1	*Cardiocondyla emeryi*	LO, PI	Lattke et al. 2016; Dominguez et al. 2016; this study
2	*Cardiocondyla mauritanica*	PI	This study
3	*Cardiocondyla minutior*	OR, PI	Donoso et al. 2014; this study
4	*Cardiocondyla wroughtonii*	SD, LO	Donoso et al. 2014; this study
5	*Linepithema humile*	PI, TU, AZ, OR	Wild 2004; Donoso et al. 2014
6	*Monomorium floricola*	OR, GU, MA, ES, LO, SU	Donoso et al. 2014; this study
7	*Monomorium pharaonis*	OR, PI, MA, GU	Donoso et al. 2014; this study
8	*Nylanderia fulva*	GU	Pazmiño-Palomino et al. 2020
9	*Paratrechina longicornis*	LR, EO, NA, SD, GU, LO, MA, SE, SU, ZC, IM, MS	Wetterer 2008; this study
10	*Pheidole megacephala*	GU, PI, IM	This study
11	*Strumigenys rogeri*	SD	Wetterer 2012
12	*Tapinoma melanocephalum*	GU, PI, NA, ES, MA, OR, PA, ZC, SU, LO	Donoso et al. 2014; this study
13	*Tetramorium bicarinatum*	PI, OR, SU	Donoso et al. 2014; this study
14	*Tetramorium lucayanum*	SD, NA, CO	Donoso et al. 2014
15	*Trichomyrmex destructor*	GU, SE	Wetterer 2009

intense; in Pichincha there is Quito, the capital of Ecuador, while in Orellana is Francisco de Orellana, also known as "El Coca", one the main entries into Ecuadorian Amazon.

Introduced tramp ants have been reported to cause negative impacts, which range from attacks to domestic animals (Aldana et al. 2013), displacement of native fauna (LeBurn et al. 2013), obstruction to human activities, and transport of pathogens (Lutinski et al. 2015). Despite their importantce to nature conservation and human well-being, the presence of these most invasive ant species in Ecuador has gone unnoticed until now. Most attention has been given to other exotic animal groups, such as the mollusks *Lissachatina fulica* (Bowdich, 1822) and *Pomacea canaliculata* (Lamarck, 1822), and American Bullfrog, *Lithobates catesbeianus* (Shaw, 1802) (Correoso 2006; Cobos et al. 2016; Ministerio del Ambiente 2019, Narváez et al. 2023). Yet, the potential negative effects that exotic ants may have on the natural environment and humans, have been ignored and should be considered for future research (Holway et al. 2002; Bertelsmeier et al. 2016; Pazmiño-Palomino et al. 2019; Cuthbert et al. 2022).

We hypothesize that the problem of invasive ants will worsen as they continue to expand into new areas to the limits of intact, native forest areas (Bertelsmeier et al. 2016; Lach 2021). For example, Francisco de Orellana, a town near Yasuni National Park, is one of the most important commercial and demographic centers in the northern Ecuadorian Amazon. The expansion of the human population and trade could aid in the dispersal of exotic ant species within that national reserve (Mestanza-Ramón et al. 2023).

Biological traits such as adaptation to anthropogenic environments, polygamy, polydomy, absence of interspecific aggression, and mutualistic relationships with Hemiptera, can also augment tramp ant species dispersal (Suárez et al. 2010). Human activities, such as trade, tourism, urbanization, and changes in land use, among other activities, will undoubtedly increase the invasive potential of non-native ants (Butchart et al. 2010; Borden and Flory 2021).

The introduction of invasive ants into the natural reserves could replace the native fauna through predation, hybridization, and competition with native ant species. This could lead to changes in ecosystem processes, biodiversity loss, and an increase of pests (Peh 2010; Siddiqui et al. 2021). This phenomenon will be aggravated by global climate change, which can influence species' distribution and forest dynamics, especially in the tropics (Bertelsmeier 2015; Siddiqui et al. 2021).

In our study, most of the records were found in areas with varying levels of disturbance, such as in urbanized regions, agroecosystems, borders of nature reserves, and inside national protected areas. We report the presence of exotic ant species from five national reserves: Yasuní National Park, Cuyabeno Wildlife Reserve, Limoncocha Biological Reserve, Cerro Blanco Protected Forest, and Río Canandé Biological Reserve. The latter two are among the last well-preserved remnants of forest along the Ecuadorian coast.

Based on our field observations, we suspect that ranger stations and tourist lodges within reserves may serve as focal points for the dispersal of exotic ant species. These sites are the gateway for tourists, park rangers, and vehicles, which could be responsible for transporting these species (Espinoza et al. 2022). Current national environmental regulations by the Ministerio de Ambiente, Agua y Transición Ecológica (MAATE) require that the construction of ranger stations in protected areas be carried out only with materials brought from outside the reserves (MAATE

2016). This is another potential source of alien species and may likely contribute to the threats faced by native organisms in national reserves.

In this study we updated the catalog of invasive ant species in continental Ecuador, identified the first country records of two globally important invasive species, and added new locality records for nine previously recorded species. We made this using open-sourced data from scientific collections and online databases that will keep growing in the future. Our initiative lays the groundwork for future research on the biology, ecological interactions, and dispersal capabilities of invasive ant species in Ecuador. With the addition of genetic data, a future study could result in a more comprehensive understanding of the invasion history and metapopulation structure of exotic ants in Ecuador. Also, if potential distributions of exotic ants were projected under various climate-change scenarios, policymakers could be informed on environmental risks. There is a pressing requirement for a national strategy involving local and national governments in Ecuador and the society as whole.

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Authors' Contributions

Conceptualization: JSB, APP. Data curation: JSB, FR, APP, AT. Formal analysis: JSB, APP, AT. Funding acquisition: APP. Investigation: JSB, APP, AT. Methodology: APP. Resources: APP, AT,AW. Supervision: JSB, APP. Visualization: JSB, APP. Project administration: APP, JSB. Software: FR, AT. Validation: AT, APP. Writing – original draft: JSB, APP, AT. Writing – review and editing: JSB, APP, AT, FR, AW.

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Supplementary Data

We provide a table containing all species records, both of the examined material and literature, together with their collection information.